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Myxomycete history and taxonomy: highlights from the past, present, and future

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Abstract—The past myxomycete legacy covers fruiting bodies preserved in fossil amber more than 35 million years ago and early contributions by Linnaeus, de Bary, and the Listers at the British Museum of Natural History (BM), among whom the Listers introduced monographs, striking watercolors, and more narrow species concepts. Macbride and Martin (University of Iowa) published illustrated myxomycete monographs with broader species concepts. The transfer of the ~9500 specimen Iowa myxomycete collection to the United States National Fungus Collections (BPI) is outlined and ~234 type specimens are listed. Also covered is Lado's recent Nomenmyx and the online resource nomen.eumycetozoa.com, which offers ~900 names for accepted myxomycete species. The current status of the BM and BPI myxomycete collections is noted, and *Didymium saturnus* provides an example of data associated with myxomycete specimens in the American Type Culture Collection. Problematic taxa are recommended for DNA sequencing to help clarify phylogenetic relationships.

Key words—fossils, herbarium, Marie L. Farr, plasmodial slime molds, systematics

The legacy of the past

Myxomycetes preserved in amber— Myxomycetes have a fossil past that dates back to stalked sporangia of *Stemonitis splendens* Rostaf. that are well preserved in Baltic amber from the Tertiary Period and Eocene Epoch approximately 35 to 40 million years ago (Domke 1952; Keller & Everhart 2008). Fossilized stalked sporangia of *Arcyria sulcata* Dörfelt & A.R. Schmidt were also found in Baltic amber from the Eocene (Dörfelt et al. 2003; Dörfelt & Schmidt 2006; Keller & Everhart 2008). The general habit of these myxomycetes are so similar to present-day species that it is apparent that morphology has changed little in 40 million years. Given the advanced fruiting body development observed in these fossils, we can assume myxomycetes have been around much longer than 40 million years.

One can imagine the dominant coniferous forests of *Pinus succinifera* (Göpp.) Conw. that thrived in a warmer subtropical climate and profusely produced resin that accumulated in cracks inside the tree, under the bark, or in wounds around the tree base. This resin eventually flowed and dripped on decaying vegetation, trapping myxomycete fruiting bodies along with a variety of arthropods and plants. The accumulation of Baltic resin (succinite) resulted from millions of years of deposition. As rivers flowed through these forests, this resinous material was carried to form today's deltaic deposits along the Baltic seacoasts at present-day Estonia, Latvia, and Lithuania. However, the Baltic amber region also includes adjacent areas in Denmark, England, the Frisian Islands, Germany, Norway, Poland, Russia (in an area called Samland, in the Kaliningrad Oblast), and Sweden.

Fossil records of fragile myxomycete structures are rare due to the transitory life cycle stages that appear briefly on surface substrata and weather away in a relatively short time. Nevertheless, the excellent state of preservation in myxomycete sporangia representing the *Stemonitales* and *Trichiales* suggests that their geological past might extend to the Paleocene some 65 million years ago when a warmer tropical climate still prevailed.

The 90–94 million year-old New Jersey Cretaceous amber deposits contain the mushroom pileus and stalk of *Archaeomarasmius leggetti* Hibbett et al. that resembles present-day *Marasmius* and *Marasmiellus* mushrooms that are marcescent, persisting and reviving under moist conditions, instead of putrescent, like many fleshy macrofungi (Hibbett et al. 1995; Hibbett et al. 1997; Hibbett et al. 2003). This geological time period has the same tree species and climatic conditions that should also support myxomycete fossils. Discovery of the more ephemeral myxomycete sporangia is remote, and calcareous members of the *Physarales*, the largest and presumably the most morphologically advanced myxomycetes, never have been recorded in the fossil record. However, wherever they are found, amber deposits should be screened by a competent taxonomist for myxomycete fossils to avoid misidentification of confusing and similar looking calicioid lichens (Keller & Everhart 2008). The geological and historical recorded past should be included as part of any review about the myxomycetes.

Early students of the Myxomycetes— The first literature on myxomycetes dates back to 1654 with Pankow's (sometimes spelled Panckow) figure and illustration of the species now known as *Lycogala epidendrum* (L.) Fr. Although Linnaeus' Species Plantarum, published in 1753, is the nomenclatural starting point for the *Myxomycetes*, his treatment of them was best summed up by Martin & Alexopoulos (1969: 18): "Linnaeus, to be sure, knew little about the fungi or slime molds, and cared less." Carl Linnaeus (1701–78), who considered

the myxomycetes to be gasteromycetous fungi (puffballs), was undoubtedly influenced by the appearance of *Lycogala* as a miniature puffball. Martin (1966) provides a more detailed account and review of these early students of the myxomycetes.

The 1800s were marked by a better understanding of the myxomycete life cycle by Heinrich Anton de Bary (1831–88) and the taxonomic advances by his student Józef Thomasz Rostafińsky (1850–1928). Earlier myxomycete taxonomists had relied primarily on the striking variation of macroscopic characteristics, whereas Rostafińsky (1874, 1875, 1876) ushered in use of microscopic characters that would largely influence later description and classification of the *Myxomycetes*. De Bary has been called the founding father of plant pathology and mycology, which also embraces myxomycology. He was the first to demonstrate myxomycete spore germination and the subsequent stages of myxamoebae, swarm cells, plasmodia, and fruitbody development. De Bary's observations provided the microscopic evidence that led to removal of the *Myxomycetes* from the fungal *Gasteromycetes* and the coinage of the name *Mycetozoa* (Martin 1958; Everhart & Keller 2008).

Arthur and Gulielma Lister, Myxomycetes, and the British Museum (Natural History, now the Natural History Museum)— The lives of the Listers (father Arthur, 1830–1908 and daughter Gulielma, 1860–1949) spanned 119 years. In the main, their world monographs [1894, 1911 (second edition), 1925 (third edition)] follow Rostafińsky's classification. The Lister publications stand as a landmark in myxomycete taxonomy, influencing many regional treatises that appeared over the following 50 years. More attention is given to the range of environmental conditions and the remarkable extent to which these factors may influence the appearance and structures of the developing fruiting body. Even so, they recognized 274 species, 101 varieties, and one form for a total of 376 taxa. The more than 60-year influence of the Listers as world authorities on myxomycete taxonomy, especially throughout Europe, resulted in a more frequent use of variety to designate differences in habit, color, and structural microscopic changes in fruiting body morphology. The 128 color and 94 black-and-white plates by Gulielma Lister in the 1925 edition are without equal and stand as a lasting tribute to her artistic skill. Because many species in 53 genera are illustrated in color, they can be easily 'picture-keyed' and correctly identified. The Listers' valuable type myxomycete specimens are deposited in the collections at The Natural History Museum (BM) formerly the British Museum (Natural History), London, United Kingdom.

Macbride, Martin, Myxomycetes, and The University of Iowa— The 1900s highlighted the active research of Thomas Huston Macbride (1848–1934) and George Willard Martin (1886–1971), who served on the faculty at the

University of Iowa (U.S.A.). Their lifetime professional careers spanned almost 100 years (1878–1971) in the Department of Botany at the university. Their field collections, laboratory research, and publications were based largely on specimens housed in the University of Iowa Myxomycete Collection that also included collections of Bethel, Bilgram, Ellis, Farlow, Gilbert, Hagelstein, Harvey, Morgan, Plunkett, Rex, Shimek, and Wingate from America and of Brandza, Japp, Meylan, and Sydow from Europe. Collections were also contributed by O.F. Cook (Liberia) and the Listers (who corresponded and exchanged specimens with Macbride).

The world monograph, "The *Myxomycetes*" by Macbride and Martin was published in 1934 shortly after Macbride's death. The preface by Macbride reads:

> To assist in meeting such inquiry and interest is the purpose of this book. For this edition it has been to the writer's great pleasure and advantage to have the assistance of his colleague, Dr. G. W. Martin: the introduction and general editing of the text is his. By enlarging our field of inquiry, the number of species presented has been greatly enlarged. New plates were needed, – all our plates are new! To the young botanists of our continent and to our contributors around the world, the present volume is especially devoted. May they fare well! T.H.M.

The monograph includes 21 plates and 568 figures, all in black and white. Gladys Baker prepared the habit sketches and a number of her diagrams were made from paraffin sections. Spores, capillitia, and other microscopic structures were drawn by Martin in pencil aided by a camera lucida and using an apochromatic oil immersion lens at a uniform magnification of 1200× to facilitate comparison of these critical characters.

Comparison of the final monographs by Macbride & Martin (1934) with the Listers (Lister 1925) show a trend away from subspecific taxa. Indeed, the Martin introduction emphasizes this trend:

> Decision as to the limits of species and genera must necessarily be a matter of personal judgment, and this is perhaps more apparent in the slime molds, because of their obvious responsiveness to environmental conditions while the fructifications are forming, than in most other groups. We have felt justified in applying a distinctive specific name to any form which shows reasonable constancy under varying conditions, even though occasional intermediate forms may appear. The multiplication of varieties has nearly if not quite reached the saturation point. Many of the varieties listed in the literature are obviously merely growth forms; some are doubtless autonomous species. If the latter, they will eventually be recognized as such; if the former, it would seem better to modify the diagnosis of the species to accommodate them, rather than to multiply names.

The 1934 book recognized a total of 59 genera, 366 species, and 40 varieties. Subjective interpretation was used in some cases to tabulate a variety designation

Fig. 1. Thomas Huston Macbride (1848–1934)
(Courtesy The Scientific Monthly)

because it is not clear whether Macbride merely mentioned the variety name in passing or actually recognized the variety as distinct. In any case the number of varieties is greatly reduced from previous myxomycete authors.

Macbride (Fig. 1), who was heralded as a passionate conservationist and served as the first president of the Iowa Park and Forestry Association, also established the Iowa Lakeside Laboratory at Lake Okoboji in 1909 (Martin 1935). Among the many other honors too numerous to mention are the facts that Macbride served as the tenth president of The University of Iowa (1914–1916) and that the building housing the University of Iowa Museum of Natural History now bears the name of Macbride Hall, dedicated in his honor shortly after his death in 1934 (Martin 1935).

Progress in the present

Martin, Alexopoulos, and The University of Iowa Myxomycete Collection— The tradition of myxomycology at the University of Iowa has involved three outstanding myxomycologists, Macbride, Martin, and Alexopoulos. The world monograph "The *Myxomycetes*" by Martin & Alexopoulos (1969) was another milestone in myxomycete nomenclature and taxonomy. These two myxomycologists worked as a team when Martin was

in retirement and Constantine John Alexopoulos (1907–86) was Chairman of the Department of Botany at the University of Iowa and later served on the faculty at the University of Texas. This book is based on the Macbride–Martin Collection at the University of Iowa that also includes additional numerous collections of C. J. Alexopoulos, Travis E. Brooks, William Bridge Cook, and Donald T. Kowalski.

Perusal and tabulation of all species descriptions yields 53 genera, 425 species, and 2 varieties. The trend here again is away from sub-specific designations, as emphasized by the following:

> One fact should be stressed. The plasmodium may develop its characteristic fruiting stage in less than 24 hours. If this occurs under conditions which cause unduly rapid drying or if repeated rains check the process, great variation may be induced. Under such influences, species which ordinarily have stalks may be sessile or nearly so, or the stalks may be inordinately long; sporangiate species may form plasmodiocarps; aethalioid forms may approach the sporangiate type; the characteristics and disposition of limy secretions may be altered; spore maturation may be checked, resulting in spore-like bodies which are much larger than fully matured spores. Cold weather, and particularly frosts, may induce similar alterations. Such variations are in large part responsible for the extensive synonymy found in the group. Great caution is indicated in describing as new specimens that are the result of such environmental responses. They are not "abnormal"; they are natural responses of the organisms involved to particular stimuli and must be so regarded. Giving them taxonomic status as named varieties serves only to complicate the nomenclature and to extend the meaning of the category variety beyond its legitimate significance. (Martin & Alexopoulos 1969: 3)

This rather long quotation captures the essence of Martin's lifelong approach to the taxonomy of the *Myxomycetes*. This trend in America toward taxonomic conservatism, broader species concepts, and recognition of fewer species was categorized as "species lumping" and those in Europe who had narrow species concepts and described many new species, often based on single collections and limited specimens, were categorized as "species splitters" (Bisby 1953).

All 41 plates and 367 figures show individual images of habits and microscopic characters of crystals, capillitium, and spores that represent a composite set of morphological features. Spores, magnified at 1000×, lack the detail of today's scanning electron microscopic images. Spore ornamentation and other spore characters used in keys relied on high dry power (430×), not the oil immersion lens. This is not apparent in the book text but is what I observed when I was a graduate student during the monograph's preparation. All color illustrations were made by Ruth McVaugh Allen using colored pencils.

The moist chamber culture technique that was introduced at the University of Iowa Mycology Laboratory by Gilbert & Martin (1933) has led to the discovery

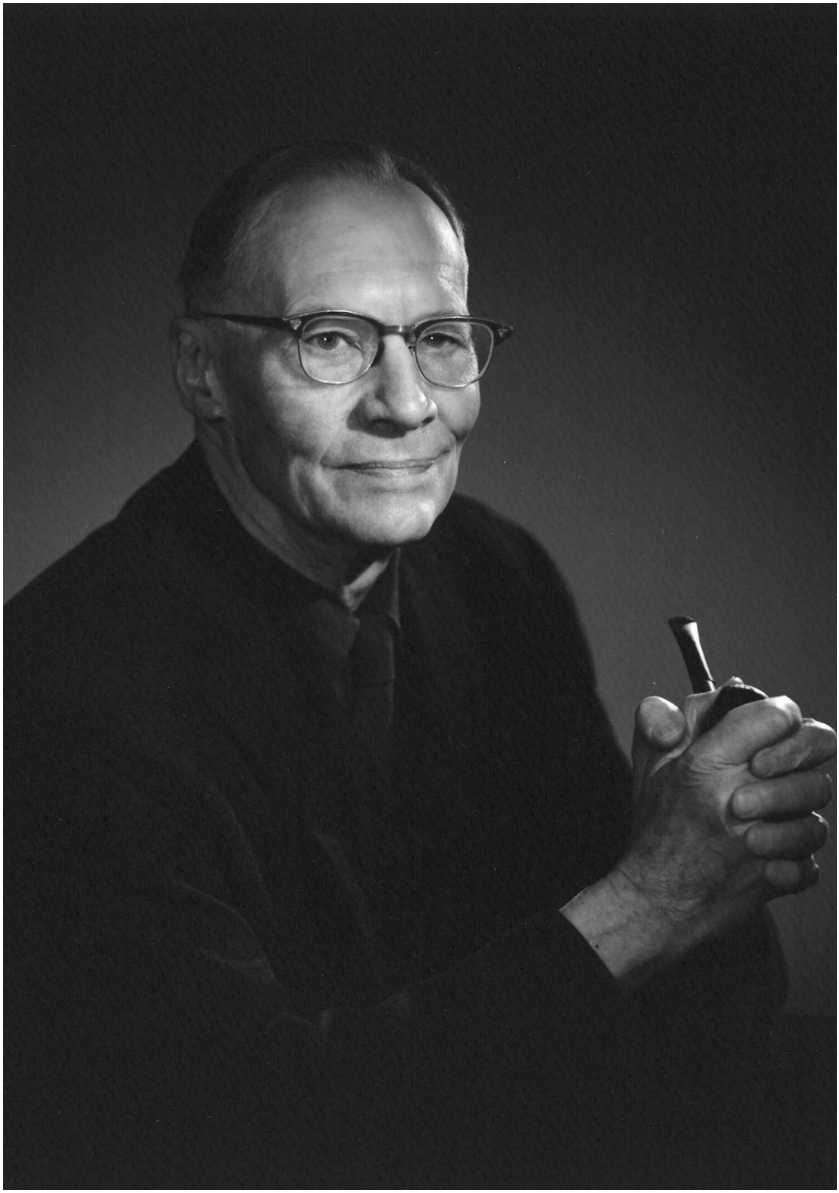

Fig. 2. George Willard Martin (1886 –1971)
(Frederick W. Kent, Iowa City, photographer)

of many new tiny myxomycetes found on the bark of living trees. *Echinostelium* de Bary, represented by only a single species, *E. minutum* de Bary, in 1874, increased to five species in 1969 (Martin & Alexopoulos 1969). *Macbrideola*, a genus named after T.H. Macbride by Gilbert (1934), described two new tiny species, *M. scintillans* H.C. Gilbert and *M. decapillata* H.C. Gilbert, obtained from the bark of living trees through moist chamber culture. Thirty-five years later *Macbrideola* was represented by five species (Martin & Alexopoulos 1969).

The chronicle of Martin's life by Lentz & Benjamin (1971) and Wells & Lentz (1973) was augmented by a personal account by Keller (1996). As a United States Army Lieutenant during World War I, Martin was slightly wounded by artillery fire while gathering intelligence on the battlefield during shelling and assaults by the Americans and Germans. During World War II he served as Chief of the Biological Laboratory at the Army Quartermaster Depot in Jeffersonville, Indiana. The Botanical Society of America recognized his extraordinary research and service and he was part of the first group to receive the Certificate of Merit. He served as Director of the Lakeside Laboratory in Iowa from 1928 to 1934. A charter member of the Mycological Society of America, Martin became its first Vice President in 1933 and President in 1944 and also served as Editor-in-Chief of Mycologia from 1950 to 1957. His experience teaching English courses at Rutgers University and his command of narrative text undoubtedly contributed to his 37-year tenure as the editor of the University of Iowa Studies in Natural History from 1934 until his death. The picture of Professor Martin (Fig. 2) was taken about the time of his retirement as head of the Department of Botany in 1955.

He was selected by the North American Flora project as author of The Myxomycetes published by the New York Botanical Garden (Martin 1949). The subsequent world monograph, (Martin & Alexopoulos 1969) is still considered the most authoritative work on the subject. This book along with his lifelong research on myxomycetes were cited as the basis for the Henry Allan Gleason Award given in 1970 to Professor Martin by the New York Botanical Garden for an outstanding recent publication in the fields of plant taxonomy, plant ecology, or plant geography.

During the course of his career he published more than 140 separate titles that included journal papers and books and spanning different groups from dinoflagellates to fungi. The broad spectrum of fungi treated included pathogenic imperfects, water molds, ascomycetes, the *Agaricales*, the resupinates of the *Homobasidiomycetidae*, bird's nest fungi, soil fungi, and tropical fungi from his trips to Colombia, Galapagos Islands, and Panama. Many collections were made of jelly fungi (*Tremellales*) and true slime molds (*Myxomycetes*) while serving as a world authority for these two groups. Most of his papers

were single-authored and his practice of not attaching his name as a coauthor to student-authored papers was followed until his death. Professor Martin was a research mentor for approximately 47 doctoral students (Wells & Lentz 1973), who represented a living testament to his impact on fungi, myxomycetes, and all who knew him professionally.

At the time of Professor Martin's death in 1971, the Macbride–Martin Myxomycete Collection at the University of Iowa numbered approximately 9500 specimens. In a letter dated March 22, 1977 I was informed by Dr. Robert L. Hulbary, Professor and Chairman of the Department of Botany, that the decision not to fill the faculty position held by Professor Martin had resulted in the transfer of the Macbride–Martin Collection of Myxomycetes, January, 1977 to the United States National Fungus Collections (BPI) located at Beltsville, Maryland.

The summer of 1972, I was asked to curate the entire myxomycete collection and compile a list of type specimens. Type specimens were kept in a separate herbarium case that included specimens in boxes as well as microscope slides carefully wrapped in tissue paper inside boxes and all were labeled as types. A list of approximately 235 types (specimens and microscope slides) was prepared from the names taken from the box labels and arranged alphabetically by genus and species. In the following list, authors' names have been corrected and presented as standard abbreviations, where necessary. The following types are now held in BPI:

Amaurochaete *comata* G. Lister & M. Brândză, *A. ferruginea* T. Macbr. & G.W. Martin, *A. minor* Sacc. & Ellis, *A. trechispora* T. Macbr. & G.W. Martin; ***Arcyria*** *annulifera* Torrend (slide only), *A. corymbosa* M.L. Farr & G.W. Martin, *A. magna* Rex; ***Badhamia*** *armillata* Nann.-Bremek., *B. cinerascens* G.W. Martin, *B. dearnessii* Hagelst., *B. gracilis* (T. Macbr.) T. Macbr., *B. iowensis* T. Macbr., *B. viridescens* Meyl.; ***Calonema*** *aureum* Morgan, *C. luteolum* Kowalski; ***Ceratiomyxa*** *morchella* A.L. Welden; ***Clastoderma*** *pachypus* Nann.-Bremek. (slide only); ***Comatricha*** *acanthodes* Alexop. (slide only), *C. aggregata* M.L. Farr, *C. amoena* Nann.-Bremek., *C. brachypus* (Meyl.) Meyl., *C. caespitosa* Sturgis, *C. extendens* Hagelst., *C. longipila* Nann.-Bremek., *C. martinii* Alexop. & Beneke, *C. mirabilis* R.K. Benj. & Poitras, *C. nodulifera* Wollman & Alexop., *C. peritricha* Nann.-Bremek., *C. reticulata* H.C. Gilbert, *C. rispaudii* Hagelst., *C. shimekiana* T. Macbr., *C. subcaespitosa* Peck, *C. suksdorfii* Ellis & Everh., *C. synsporos* Alexop.; ***Diachea*** *silvipluvialis* M.L. Farr, *D. thomasii* Rex; ***Diacheopsis*** *depressa* K.S. Thind & T.N. Lakh.; ***Dianema*** *aggregatum* Kowalski, *D. andersonii* Morgan, *D. harveyi* Rex, *D. nivale* (Meyl.) G. Lister; ***Dictydium*** *rutilum* G. Lister; ***Diderma*** *antarcticum* (Speg.) Sturgis (slide only), *D. brooksii* Kowalski, *D. cinereum* Morgan, *D. corrugatum* T.E. Brooks & H.W. Keller, *D. darjeelingense* K.W. Thind & H.S. Sehgal, *D. indicum* K.S. Thind & H.S. Sehgal, *D. mussooriense* K.S. Thind & Manocha, *D. nigrum* Kowalski, *D. platycarpum* Nann.-Bremek., *D. roanense* (Rex) T. Macbr., *D. rugosum* (Rex) T. Macbr., *D. subcaeruleum* Kowalski, *D. subdictyospermum* (Rostaf.) G. Lister, *D. subincarnatum* Kowalski; ***Didymium*** *aurantipes* T.E. Brooks & Kowalski, *D. discoideum* K.S. Thind & H.S. Sehgal, *D. floccosum* G.W. Martin, K.S. Thind & Rehill, *D. fulvum* Sturgis, *D. labyrinthiforme*

G.W. Martin, Lodhi & N.A. Khan, *D. leoninum* Berk. & Broome, *D. nivicola* Meyl., *D. orthonemata* H.W. Keller & T.E. Brooks, *D. ovoideum* Nann.-Bremek., *D. parietale* G.W. Martin & T.E. Brooks, *D. rugulosporum* Kowalski, *D. saturnus* H.W. Keller, *D. synsporon* T.E. Brooks & H.W. Keller, *D. verrucosporum* A.L. Welden; ***Echinostelium*** *cribrarioides* Alexop., *E. elachiston* Alexop.; ***Enerthenema*** *melanospermum* T. Macbr. & G.W. Martin, *E. syncarpon* Sturgis; ***Hemitrichia*** *karstenii* (Rostaf.) Lister, *H. montana* (Morgan) T. Macbr., *H. obrussea* Meyl., *H. paragoga* M.L. Farr; ***Lamproderma*** *biasperosporum* Kowalski, *L. cristatum* Meyl., *L. fusiforme* Kowalski, *L. gulielmae* Meyl., *L. pulchellum* Meyl., *L. robustum* Ellis & Everh., *L. splendens* Meyl., *L. tuberculospora* M.L. Farr, *L. verrucosum* G.W. Martin, K.S. Thind & Sohi; ***Leocarpus*** *fulvus* T. Macbr.; ***Lepidoderma*** *crustaceum* Kowalksi; ***Licea*** *applanata* Kowalski, *L. biforis* Morgan, *L. denudescens* Keller & Brooks (paratype: TEB2502, as *L colloderma* ined.). *L. erecta* K.S. Thind & Dhillon, *L. fimicola* Dearn. & Bisby, *L. pedicellata* (H.C. Gilbert) H.C. Gilbert, *L. perexigua* T.E. Brooks & H.W. Keller, *L. pseudoconica* T.E. Brooks & H.W. Keller, *L. pumila* G.W. Martin & R.M. Allen, *L. punctiformis* G.W. Martin, *L. scyphoides* T.E. Brooks & H.W. Keller, *L. synsporos* Nann.-Bremek. (slide only), *L. tuberculata* G.W. Martin; ***Lycogala*** *exiguum* Morgan; ***Macbrideola*** *decapillata* H.C. Gilbert, *M. scintillans* H.C. Gilbert; ***Metatrichia*** *horrida* Ing; ***Oligonema*** *aeneum* P. Karst., *O. fulvum* Morgan; ***Orthotricha*** *microcephala* Wingate; ***Paradiacheopsis*** *cribrata* Nann.-Bremek. (slide only); ***Perichaena*** *brevifila* T.E. Brooks & H.W. Keller, *P. quadrata* T. Macbr., *P. syncarpon* T.E. Brooks; ***Physarina*** *echinospora* K.S. Thind & Manocha; ***Physarum*** *auripigmentum* G.W. Martin, *P. bethelii* G. Lister, *P. confertum* T. Macbr., *P. dictyosporum* G.W. Martin, *P. galbeum* Wingate, *P. limonium* Nann.-Bremek., *P. maculatum* T. Macbr., *P. mennegae* Nann.-Bremek., *P. metallicum* Berk., *P. mortonii* T. Macbr., *P. nicaraguense* T. Macbr., *P. nudum* T. Macbr., *P. oblatum* T. Macbr., *P. pulcherrimum* Berk. & Ravenel, *P. retisporum* G.W. Martin, K.S. Thind & Rehill, *P. rubronodum* G.W. Martin, *P. serpula* Morgan, *P. spinulosum* K.S. Thind & H.S. Sehgal, *P. tessellatum* G.W. Martin & M.L. Farr, *P. tropicale* T. Macbr., *P. variabile* Rex, *P. variegatum* K.S. Thind & Dhillon; ***Schenella*** *microspora* G.W. Martin, *S. simplex* T. Macbr.; ***Stemonitis*** *carolinensis* T. Macbr., *S. herbatica* Peck, *S. inconspicua* Nann.-Bremek., *S. morganii* Peck, *S. mussooriensis* G.W. Martin, K.S. Thind & Sohi, *S. nigrescens* Rex, *S. smithii* T. Macbr., *S. uvifera* T. Macbr., *S. virginiensis* Rex, *S. webberi* Rex; ***Trichia*** *andersonii* Rex, *T. cascadensis* H.C. Gilbert, *T. crateriformis* G.W. Martin, *T. erecta* Rex, *T. mirabilis* Nann.-Bremek., *T. reniformis* Peck; ***Tubifera*** *papillata* G.W. Martin, K.S. Thind & Sohi; ***Wilczekia*** *evelinae* Meyl.

Marie L. Farr and the United States National Fungus Collections—Farr received her doctorate from the University of Iowa in 1957 under the direction of Professors G.W. Martin and C.J. Alexopoulos. Thereafter, she spent her professional career at BPI (1958–89), during that time accumulating myxomycete collections from South American countries and the Caribbean Islands between the Tropics of Cancer and Capricorn, a geographic area designated as the Neotropics (Farr 1976). This led to the publication of No. 16 of the Flora Neotropica Monographic Series, a volume devoted to the *Myxomycetes*. The approximately 280 myxomycete species recorded in Flora Neotropica 16 also includes myxomycetes from Florida state (U.S.A.). This myxomycete monograph includes not only the standard dichotomous keys but also offers the first available synoptic keys for the identification of myxomycete species.

It is especially appropriate here to recognize Farr's publications, travels, and collections in the Caribbean Islands and Brazil. She collected myxomycetes during 16 months (1954–55) on the Caribbean island of Jamaica, after which she published an artificial identification key to 26 genera of Jamaican slime-moulds and separate keys to 104 species and 4 varieties (Farr 1957). Recife and the Institute of Mycology at the University of Recife in Brazil was the location of the IMUR herbarium where Farr studied myxomycetes and published a list of 21 genera and 67 species during a stay of several months (Farr 1960). She followed this with an illustrated key to the myxomycetes of South America published in English (Farr 1968) that was the principal South American resource for myxomycete identification. She also participated in the Bredin–Archbold–Smithsonian Biological Survey of Dominica in 1966 that resulted in 500 myxomycete specimens collected in the field (63 from moist chamber cultures), representing 96 myxomycete taxa (Farr 1969).

The first field guide to myxomycetes was written by Farr as part of the How to Know Pictured Key Nature Series launched by Harry E. Jaques in 1937 at Iowa Wesleyan University (Farr 1981). This spiral-bound paperback, even though out of print, is still an excellent source for beginners to identify the more common myxomycete species with dichotomous keys.

Farr updated the Martin & Alexopoulos 1969 monograph in 1983 to provide more current references and information in the introductory topical sections, to reclassify some subclasses, families, and genera, and to add keys and discuss 47 genera under a new title, The genera of *Myxomycetes* (Martin et al. 1983). The 41 plates and 367 figures are the same as those published in the previous world monograph (Martin & Alexopoulos 1969).

Many collections from Dr. D.H. Mitchel and S.W. Chapman, mostly from higher elevations in Colorado, were deposited at the Denver Botanic Garden and BPI in cooperation with Farr (Mitchel et al. 1980). A lifetime of contributions by Dr. Farr to myxomycete taxonomy merits special recognition.

Carlos Lado and Nomenmyx— In 2001, Lado published Nomenmyx, which involved the monumental task of searching the literature for names of myxomycete species. Of the 4000 names applied to various myxomycete taxa he uncovered, 900 are current names for accepted species. These names are now in a database that can be updated over time with the addition of new names and which has been developed into the online resource nomen.eumycetoza.com. Another welcome future addition will be information on types assigned to each myxomycete taxon, the herbarium where the type was deposited, and the transcription of the original description, its geographical distribution, its substratum, and synoptic keys.

Lado (2001) recognized 57 genera and approximately 900 species. Comparison of subspecific taxa was not included but the number of genera closely parallels

that of Nannenga-Bremekamp (1991). As Nomenmyx is strictly a compilation of names that did not involve examination of type specimens, some taxa listed may not represent legitimate myxomycete species; thus rigorous type studies will help refine myxomycete taxonomy. Fortunately some generic names more familiar to students of myxomycetes have been conserved in their more recent usage, including *Amaurochaete* conserved against *Lachnobolus*, *Ceratiomyxa* conserved against *Famintzinia*, *Hemitrichia* conserved against *Hyporhamma*, *Reticularia* conserved over *Enteridium*, and *Tubifera* conserved over *Tubulifera*. All taxonomists are urged to peruse all previous myxomycete names to avoid publishing duplicate names for species new to science.

The promise of the future

Myxomycetes and herbaria— Preservation of myxomycete collections in the past usually involved exposure to para-dichlorobenzene (PDB) and/or naphthalene (organic chemical compounds present in mothballs) used to protect against insects, mites, and fungal contaminants. The Macbride–Martin Collection at the University of Iowa was treated with mothballs for many years before concerns that PDB was a potential carcinogen. Furthermore, Gray & Alexopoulos (1968: 228), recommend PDB for use "…in the herbarium case or drawer in which the specimens are stored." This was standard practice for many herbaria of the mid-twentieth century. However, combination of age and treatment with organic agents appears to fragment DNA in older type myxomycete specimens, which impedes DNA amplification for taxonomic molecular studies.

Schenella simplex T. Macbr. was considered a myxomycete for more than 100 years until light microscopy, scanning electron microscopy, and DNA analysis revealed it to be a fungal gasteromycete (Estrada-Torres et al. 2005). The holotype specimen (BPI 839197) was included in a morphological comparison with specimens recently collected in Mexico. DNA extraction was successful for one Mexican specimen, and its nuclear profile most closely matched the fungus *Geastrum saccatum* Fr. whose sequence differed greatly from true myxomycete sequences. Attempts to extract and analyze DNA from the holotype specimen (BPI 839197) using the same molecular techniques were unsuccessful, as the DNA had fragmented and deteriorated over time, either due to age or external treatment with PDB or both (Dennis Miller pers. comm.).

Odell & Perkins (1976) observed that PDB adversely affects life cycle stages of *Didymium squamulosum* (Alb. & Schwein.) Fr. by placing PDB crystals on Petri dish lids, inverting the culture dish, and noting that myxamoebae died in 18 hours leaving ghost-like remnants on the agar surface. Similar treatment of plasmodia stopped protoplasmic streaming within 40 seconds and caused death after 20 minutes. Additional experiments showed that spores from sporangia

of *Comatricha nigra* (J.F. Gmel.) J. Schröt., *Trichia varia* (J.F. Gmel.) Pers., and *T. favoginea* (Batsch) Pers. collected on decaying wood showed a consistent reduction in the percentage of germinated spores when exposed to vapor from PDB crystals. Furthermore, after exposure to PDB, spores were abnormally wrinkled and distorted in shape. These experiments also showed that the percentage of spore germination decreased markedly after only three months. Odell & Perkins (1976) concluded that PDB should not be used in herbarium cases where myxomycete fruiting bodies are stored. Thus, more recently, herbarium managers have had discussions about using type specimens for possible molecular analysis. There is special concern that tiny fruiting bodies of many myxomycete species should not be subjected to destructive techniques used for DNA analysis.

More recent policy changes at BPI will require proof of experience and protocols before granting permission for specimens to be destructively sampled (Amy Rossman, pers. comm.). One possible option is to select an epitype from more recently collected specimens similar to the *Schenella* collections from Mexico (Estrada-Torres et al. 2005). Future molecular techniques may also be developed that can overcome the barriers of age caused by fragmented DNA.

If at all possible, myxomycete type specimens should be deposited in national herbaria that can provide long-term curation and make specimens available to the scientific community. The Natural History Museum (BM) still has a standing policy that specimens, including types, are generally not sent on loan; however, applications to request "invasive sampling" if approved can result in the loan of a small fragment of a fruiting body for SEM observation or DNA extraction. There is justifiable concern that myxomycete fruiting bodies are too small, brittle, and subject to possible damage when sent by mail.

The Lister Myxomycete Collection at BM— The majority of the Lister Myxomycete Collection is housed at BM but a substantial number of specimens are also deposited at the Herbarium, Royal Botanic Garden, Kew (K). Plans are in place to make more information on myxomycete specimens at both BM and K more easily accessible to users. The future of the Lister specimens currently involves the British Mycological Society (BMS) because it is the owner (including copyrights) of the notebooks with the originals of the plates for the monograph and many more unpublished sketches and partly colored illustrations. These notebooks are kept at BM but are administered independently by the library team and not by the Botany Department, which owns and curates only the specimens and microscopic slides. Label information and macro-images of the types will become available on the Internet within the next two years (Holger Thüs, pers. comm.). Consultation with appropriate curators is encouraged to coordinate access to the Lister illustrations and specimens.

The United States National Fungus Collections (USNFC)— The USNFC has a herbarium, a library and extensive databases and web resources that serve as a national and international resource. It is managed under the Systematic Mycology and Microbiology Laboratory (SMML), a federal laboratory of the US Department of Agriculture. There is a good overview of the resources with links to each at http://nt.ars-grin.gov/sbmlweb/fungi/index.cfm. The direct link to the database search pages is found at http://nt.ars-grin.gov/fungaldatabases.

The USNFC herbarium, referred to as BPI (BPI = Bureau of Plant Industry), houses more than one million specimens. About 760,000 herbarium specimens have already been entered into the specimen database, including the *Uredinales* (rusts, 186,925), *Agaricales* sensu lato (45,637 specimens; 718 types), *Ustilaginales* (smuts, 31,175), *Polyporales* (polypores, 91,976), *Deuteromycetes* (imperfect fungi, 127,298), *Ascomycetes* (172,723), and C.G. Lloyd collections (57,086, including myxomycetes) and thus covering most fungi important to agriculture.

BPI is constantly growing and the database is updated accordingly. The BPI Myxomycete Collection, now numbering between 50,000 and 60,000, ranks as the largest in the world. These specimens have been bar-coded (with 12,532 records indexed) and are available on-line at http://nt.ars-grin.gov/fungaldatabases/specimens/specimens.cfm.

The Myxomycete Collection of C.J. Alexopoulos at the University of Texas was transferred to BPI and contains specimens from the state of Texas, U.S.A., Costa Rica, and Greece, along with the D.R. Reynolds collections from the southeastern Asian countries of Thailand, Burma, and the Philippines. The entire Brooks Myxomycete Collection was also transferred to BPI. Many other collectors have deposited myxomycete collections at BPI, but in far fewer numbers.

The American Type Culture Collection— The importance of spore-to-spore culture of myxomycetes and the deposit of living cultures with the United States American Type Culture Collection (ATCC) provides future source materials for scientific experimentation, genetic discovery, and species validation. Good myxomycete taxonomic practice should include the spore-to-spore cultivation of proposed new taxa (See also "Importance of Spore-to-Spore Cultivation and Living Cultures – A Biological Standard," Keller 1996).

The mission of ATCC (www.atcc.org), a private nonprofit biological resource center and research organization, is to acquire, authenticate, preserve, develop, standardize, and distribute biological materials and information for the advancement and application of scientific knowledge. The ATCC Myxomycete Collection (excluding <50 protostelid and >400 dictyostelid strains) is represented by 36 species and slightly less than 200 strains, including the following:

Arcyria elaterensis Mulleavy, *Badhamia gracilis* (T. Macbr.) T. Macbr., *Clastoderma debaryanum* A. Blytt, *Comatricha laxa* Rostaf., *Cribraria violacea* Rex, *Diachea leucopodia* (Bull.) Rostaf., *Didymium difforme* (Pers.) Gray, *D. iridis* (Ditmar) Fr., *D. nigripes* (Link) Fr., *D. squamulosum* (Alb. & Schwein.) Fr., *Echinostelium arboreum* H.W. Keller & T.E. Brooks, *E. coelocephalum* T.E. Brooks & H.W. Keller, *E. minutum* de Bary, *Metatrichia vesparium* (Batsch) G.W. Martin & Alexop., *Physarum cinereum* (Batsch) Pers., *P. compressum* Alb. & Schwein., *P. didermoides* (Pers.) Rostaf., *P. flavicomum* Berk., *P. melleum* (Berk. & Broome) Massee, *P. polycephalum* Schwein., *P. pusillum* (Berk. & M.A. Curtis) G. Lister, *P. rigidum* (G. Lister) G. Lister, *P. roseum* Berk. & Broome, *Stemonitis flavogenita* E. Jahn, *Willkommlangea reticulata* (Alb. & Schwein.) Kuntze

Each accessioned strain is assigned an ATCC number with associated information about the live culture and the origin of the collection. *Didymium saturnus* H.W. Keller is presented as an example (Keller 1970):

> ATCC® Number, Order this item, 64178™, Organism, *Didymium saturnus* H.W. Keller, Designations, HWK 132, Isolation, Oat straw, Iowa, Depositors, H.W. Keller, Biosafety Level, 1, Shipped, frozen, Growth Conditions, ATCC medium: Corn meal agar, half-strength, Temperature: 24.0°C, Duration: grown with *Escherichia coli* ATCC 23437, Permit/Forms, In addition to the MTA mentioned above, other ATCC and/or regulatory permits may be required for the transfer of this ATCC material. Anyone purchasing ATCC material is ultimately responsible for obtaining the permits. Please click here for information regarding the specific requirements for shipment to your location, Type Strain, yes, References, 13457: Keller HW. *Didymium saturnus*, a new myxomycete occurring on straw stacks. Mycologia 62: 1061–1066, 1970. Three other collections are also available as live, two-membered cultures deposited by HWK as ATCC 64199 *Badhamia rhytidosperma* H.W. Keller & Schokn. (Keller & Schoknecht 1989c); ATCC 64200 *Didymium annulisporum* H.W. Keller & Schokn. (Keller & Schoknecht 1989a); ATCC 64201 *Badhamia spinispora* (Eliasson & N. Lundq.) H.W. Keller & Schokn. (Keller & Schoknecht 1989b). Hardcopy books are no longer available thus relevant information can be accessed online or by telephone. Deposit of myxomycete live cultures still is possible and relevant information can be found at the ATCC website. Specific criteria can be viewed online but consideration should be given as follows: "The expected demand or need for all potential deposits is reviewed and prioritized with input from the scientific community and is now a key factor in our acquisition protocol."

DNA sequencing of problematic myxomycete taxa— Future directions using DNA sequencing techniques will surely unlock many phylogenetic mysteries among the five myxomycete orders (*Echinosteliales, Liceales, Trichiales, Stemonitales, Physarales*) plus a number of genera difficult to classify. Some of these perplexing myxomycete taxa are monotypic (monospecific) genera with a distinctive suite of characters. Several examples will serve to pinpoint the taxonomic problems and to suggest a priority list of taxa that should receive a higher priority for DNA sequencing.

Minakatella longifila G. Lister is a monotypic genus that has resided in the *Trichiales* since described in 1921 within *Arcyriaceae,* a family with tubular (hollow) capillitial threads; the Listers (1925) considered *Minakatella* close to

Perichaena. Martin and Alexopoulos (1969) included the genus in *Dianemaceae* (*Dianemataceae*), emphasizing the apparent solid character of the capillitial threads. After ultrastructural evidence showed clearly that the capillitial threads of *Minakatella* were hollow, it was therefore transferred to the family *Trichiaceae* (Keller et al. 1973).

Nannenga-Bremekamp (1982) used polarized light and the birefringent property of spores and capillitium that triggered taxonomic changes for *Minakatella*. The lack of birefringence of the capillitial threads led to removal of *Minakatella* from *Trichiales* and establishment of a new family, *Minakatellaceae,* in the *Liceales*. Birefringence of the capillitium using the Nannenga-Bremekamp data is not constant (present and absent) within *Trichiales,* however, as demonstrated by *Arcyria* and *Perichaena* capillitial threads with little or no birefringence and *Trichia* and *Hemitrichia* with the highest measured levels of birefringence, all genera are still retained in the *Trichiales*. Ing (1999: 365) does not follow Nannenga-Bremekamp's taxonomy, although he recognized her taxonomic rank of the *Minakatellaceae* in the *Trichiales*. This is an extreme example of the application of "tyranny of a character" or "taxonomic tinkering" that has led to taxonomic confusion, proliferation of families, and the need for DNA analysis to help solve the final disposition of questionable taxa.

More taxa that should be considered a higher priority for DNA analysis because of uncertain taxonomic position are: *Kelleromyxa fimicola* (Dearn. & Bisby) Eliasson, *Listerella paradoxa* E. Jahn, *Protophysarum phloiogenum* M. Blackw. & Alexop., and *Trabrooksia applanata* H.W. Keller. These taxa are rare and seldom collected, for example, the occurrence of fruiting bodies of *K. fimicola* on herbivorous dung, *L. paradoxa* on *Cladonia* lichens, and *T. applanata* on the bark of living trees (especially *Juniperus virginiana* L.). This requires due diligence to find specimens in specific habitats capable of yielding positive results for DNA analysis. More taxa that would help clarify generic positions include *Barbeyella minutissima* Meyl., *Calomyxa metallica* (Berk.) Nieuwl., *Cornuvia serpula* (Wigand) Rostaf., *Badhamiopsis ainoae* (Yamash.) T.E. Brooks & H.W. Keller, *Erionema aureum* Penz., *Leocarpus fragilis* (Dicks.) Rostaf., and *Physarella oblonga* (Berk. & M.A. Curtis) Morgan. These and other taxa would provide valuable information for species currently granted an uncertain taxonomic status. The future of myxomycete biosystematics will depend more and more on DNA analysis, and I hope this will come sooner rather than later.

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